

The University of Chicago

ORIGIN AND DEVELOPMENT OF VASCULAR
SYSTEM OF LYCOPODIUM
LUCIDULUM

A DISSERTATION

SUBMITTED TO THE FACULTY
OF THE OGDEN GRADUATE SCHOOL OF SCIENCE
IN CANDIDACY FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

BY

JAMES JESSE TURNER

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Reprinted from
THE BOTANICAL GAZETTE, Vol. 78, No. 2, October, 1924



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ORIGIN AND DEVELOPMENT OF VASCULAR SYSTEM OF LYCOPODIUM LUCIDULUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 323

JAMES JESSE TURNER

(WITH SEVEN FIGURES)

Comparatively few original papers have been published which deal with the anatomy of the sporophyte of *Lycopodium*. Of these, the later ones deal mainly with the structures of the fully developed stele, and only the earlier ones have discussed the origin and development of the tissues. Occasional brief references have been found, and these will be considered in their proper connection in the body of the paper.

In view of these facts, it has been the object of this investigation, in so far as was possible, to bring our knowledge of the origin and development of the vascular tissues, of at least one species, up to date. *Lycopodium lucidulum* Michx. was chosen as representative of the more primitive group of the genus. This species is too familiar to need any description, except to say that the alternating groups of sporophylls and vegetative leaves enable one to make a fairly accurate estimate of the age of any particular portion of the stem. The material for the investigation was supplied from northeastern Ohio by Professor JESSIE M. JEROME of Hiram College.

Stele

As early as 1846, NÄGELI (7), in his researches on the growing apices of plants, examined the apex of *L. clavatum*. He figures a very definite apical cell. He noted the simultaneous differentiation of the woody strands and the leaf traces, and concluded, not without considering other possibilities, that each strand passes off into a leaf trace. He refuted the impression, then current and still accepted in some places, that the vascular cylinder consists of a single bundle, and pointed out that it was made up of as many bundles as there are centers of lignification. In 1855 CRAMER

(2) studied the apex of *L. Selago*, and pointed out that there is no relation between the number of leaves in a single turn of the spiral and the number of strands making up the stele. In 1872 HAGELMAIER (3) published a series of articles in which he discussed the anatomy of the stem and the development of the apical region. His conclusion was that there is an apical group of from two to four cells that give rise to tissues of the stem. That same year STRASBURGER (8) gave an account of the apical development of *L. Selago*. His conclusion was that a single apical cell gives rise to the dermatogen and the periblem, and that one or two deeper cells give rise to the plerome. Later (9) he states that all the tissues of the stem arise from a single apical group. He figures three initials in transverse section and two in longitudinal section. Since that time, four papers have appeared on the anatomy of different species of *Lycopodium*, but they offer no considerable contribution to our knowledge of the development of the tissues (4, 5, 6, 10).

In the present investigation of *L. lucidulum*, the writer has never been able to trace the origin of the stem tissues to a single apical group, much less to a single apical cell. At the center of the apex there is a surface group of cells, numbering from three to five or possibly more, that by their activity give rise to the dermatogen and the periblem. Immediately below these is another group of about the same number which gives rise to the plerome. It is with this last group that we are concerned in the study of the origin of the stele. They divide both by anticlinal and by periclinal walls, but the anticlinal divisions are much more numerous at first. As a result, a lengthwise section of the cylinder shows a very blunt apex. The differentiation of the tissue systems is very rapid; 0.5 mm. below the extreme apex of the stem, it is possible to distinguish the groups which give rise to xylem from those which give rise to phloem. It seemed best to give names to these groups, and I have called the former prexylem and the latter prephloem. At this same level, differentiation is evident in the individual prexylem groups. The cells from which the protoxylem differentiates are much smaller and stain more deeply than those from which the metaxylem differentiates. On the other hand, those cells which, from their position, must be prephloem cannot be distinguished from the pericycle.

Throughout the entire period of development, the differentiation of the phloem lags behind that of the xylem. In material which was fixed in November, the older portion of the last summer's growth showed the first protoxylem well lignified, while the pre-phloem groups can be distinguished from the pericycle only by a slight difference in the intensity of the stain (fig. 1).

The usual number of xylem groups is six, although there are numerous variations, ranging from five to eight, both in the same

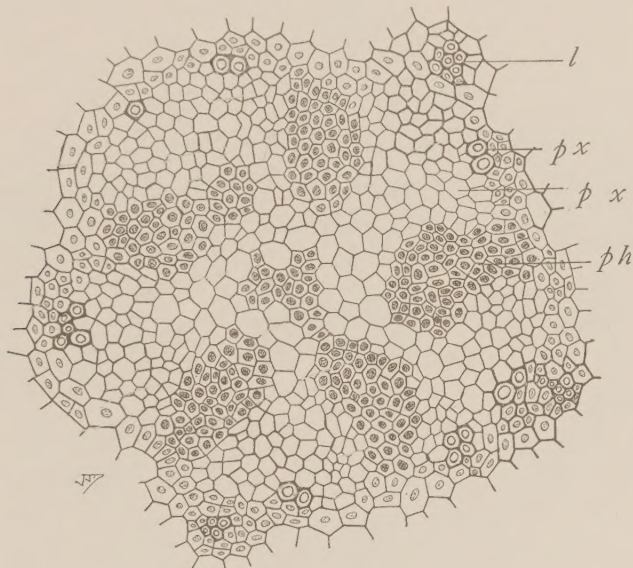


FIG. 1.—Cross-section through last summer's growth: *p-x*, prexylem; *ph*, phloem; *px*, protoxylem; *l*, leaf trace.

stem at different levels and in different stems. In some slides of sporelings, kindly loaned me by Mr. E. A. SPESSARD, the xylem groups range from two to four.

The arrangement is typically radial, the xylem groups alternating with phloem groups, and meeting more or less completely in the center. Sometimes a mass of phloem occupies the central portion. This, however, always connects with one of the peripheral bands, although in particular sections it may show as an isolated group. The differentiation of both xylem and phloem is centripetal. In my opinion the stele should be considered as a truly radial stele and not as a gamostele, either phylogenetically or ontogenetically.

In the early part of the second year, the remaining protoxylem lignifies and elongation practically ceases. The actual number of protoxylem elements is very small, if by protoxylem is meant elements with spiral or annular thickenings. From a study of developing tissues, it would seem that there is no fixed line between protoxylem and metaxylem, but that the particular type of thickening is merely a function of elongation. CHAMBERLAIN (1) calls

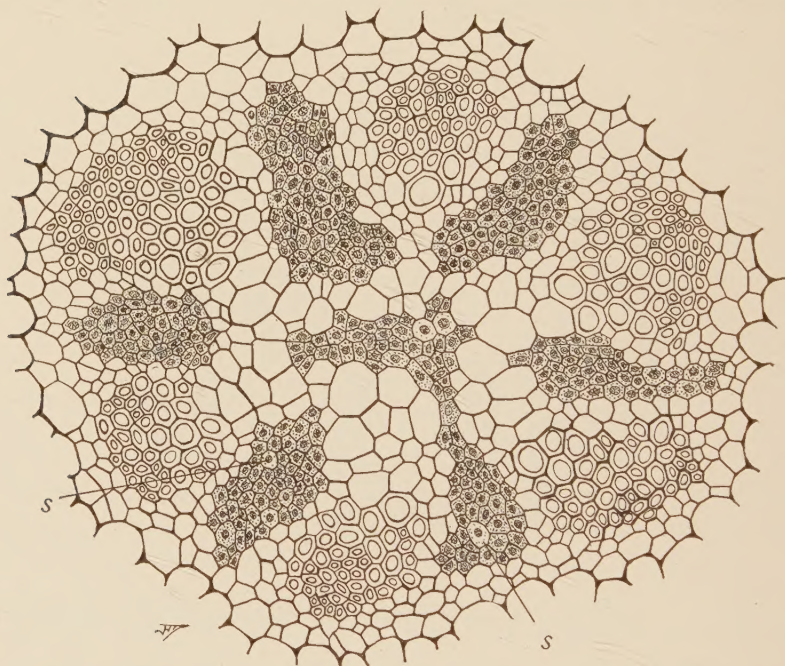


FIG. 2.—Cross-section through portion of stem two years old: lignification of xylem well along; differentiation of phloem beginning; s, differentiating sieve tube.

attention to pitted tracheids in what may fairly be called the protoxylem of the sporelings of *L. scariosum*. By the end of the second year, from two-thirds to three-fourths of the metaxylem is lignified. At this time occasional cells in the phloem groups show, by the lighter staining of the cytoplasm and nuclei, that they are differentiating into sieve tubes. I was not able to demonstrate the presence of any fully developed sieve tubes with sieve plates higher in the stem than the three-year old portion (fig. 2).

In the third year the lignification of the xylem is completed, and fully developed sieve tubes appear. In this particular species of *Lycopodium*, by far the larger part of the metaxylem consists of pitted tracheids; the smaller ones with uniseriate circular pits, the larger ones with oval multiseriate pits. Sclariform tracheids occur, but they are few in number. It is probable that the sclariform tracheids are a modified form of the pitted tracheids, in which

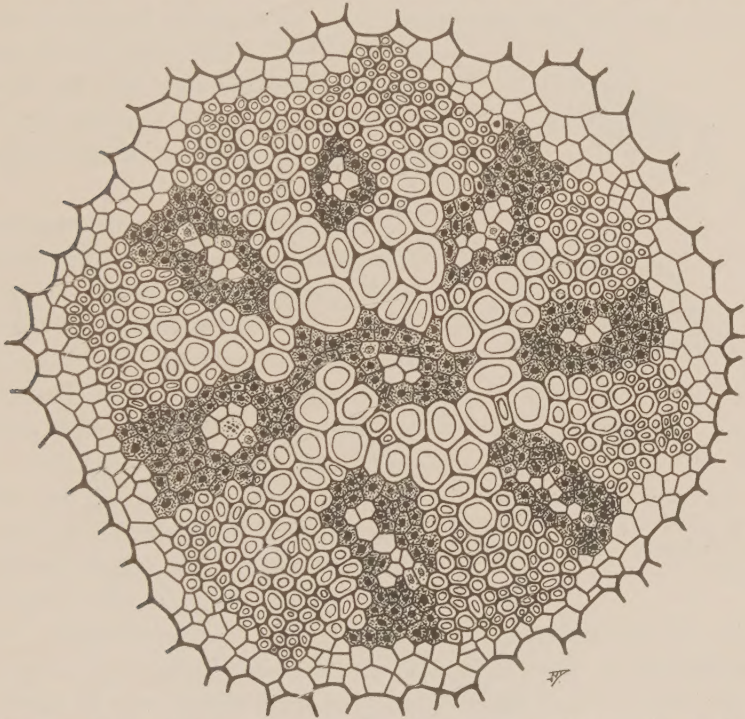


FIG. 3.—Section through three-year old portion of stem, showing completed stele

the pits are extremely elongated. Tracheids were seen which were pitted at one end and sclariform at the other, with a transition between the two forms of thickening.

The sieve tubes occupy a narrow strip in the central portion of the phloem. I could not determine that there was any definite order in their differentiation. Sometimes the first tube appeared close to the outer edge of the phloem, and sometimes close to the center of the mass. The sieve plates are scattered over the walls, and vary greatly in size (fig. 3).

Leaf strand

The leaf primordium starts as a single cell. This cuts off lateral cells and then a basal cell, but the resulting leaf is not wholly a product of these cells. The initiation of growth in the primordium seems to act as a stimulus to the surrounding tissues. Cells are activated on all sides, extending as far on the outside as the base of the preceding leaf. As a result, at the apex of the stem the leaves succeed one another without any visible length of stem intervening. It is only by the later elongation of the stem that the leaves are separated. This accounts for the decurrent leaf bases of the mature leaves (fig. 4).

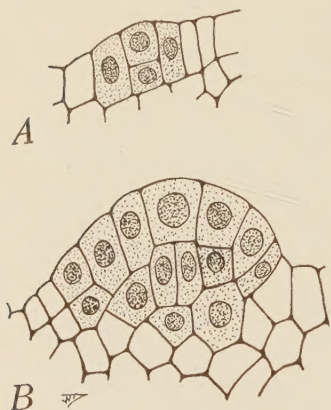


FIG. 4.—Leaf primordium: *A*, first divisions; *B*, involving of deeper layers in development of leaf.

The activation proceeds downward from the base of the developing leaf, involving deeper and deeper layers of cells. The progression in this direction is much slower, and does not reach the stele until some time after the desmogen strand is well differentiated in the leaf base (fig. 5).

The differentiation of the desmogen strand, by repeated longitudinal divisions without the transverse divisions which occur in the adjacent cells, is first evident in the base of the leaf primordium. The progression is, from this time on, both acropetal and basipetal. Acropetally, it just about keeps pace with the growth of the leaf; it never quite reaches the apex. The tip of the mature leaf is without vascular elements. Basipetally, the differentiation of the desmogen strand progresses toward the desmogen strand of the stele, meeting it some distance down the side, at an acute angle. The primordium arises without any reference to the location of the protoxylem groups. In the downward differentiation, if the desmogen strand happens to be opposite a phloem group, it swings to one side and joins with the adjacent protoxylem group. The lignification of the foliar strand proceeds in the same way.

The first thickening appears in the cells of the leaf base. By the time the first vessel has joined with the stele, lignification has begun

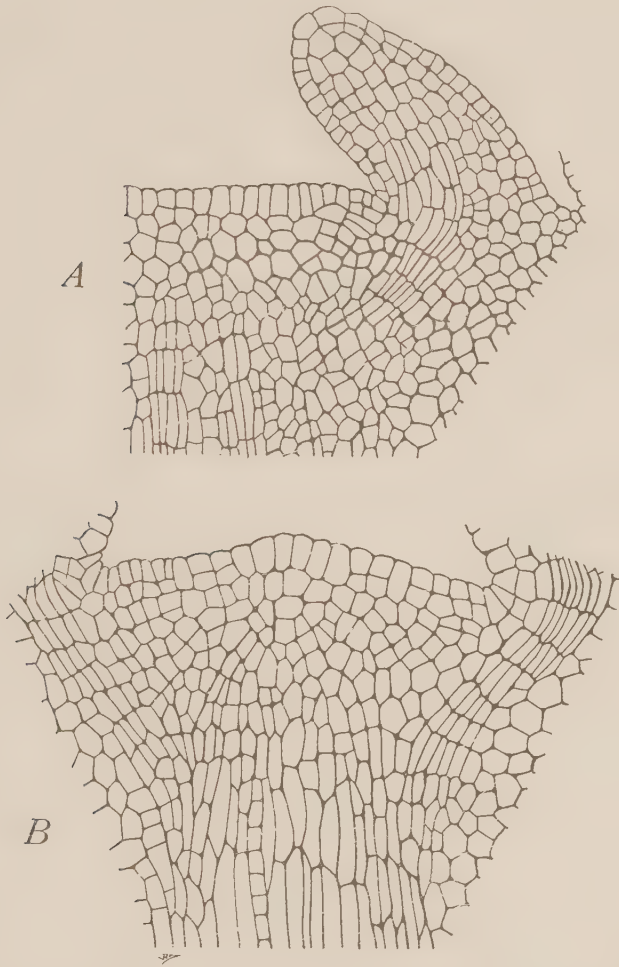


FIG. 5.—Developing strand of leaf: *A*, strand in leaf base only; *B*, connecting of strand with stele.

in other elements in the leaf base. Considerably more lignification takes place in the leaf and upper portion of the leaf trace than in that part of the trace which makes connection with the stele. A

cross-section of the leaf trace well out in the cortex shows about twice as many lignified cells as the same trace after it has passed through the endodermis of the stele (fig. 6).

The differentiation of the bundle itself begins in the center. The first lignified cell does not always occupy the exact center of the bundle, but always, so far as could be observed, within one or two cells of it. The lignification proceeds outward about equally in all directions, and is complete before the end of the first year.

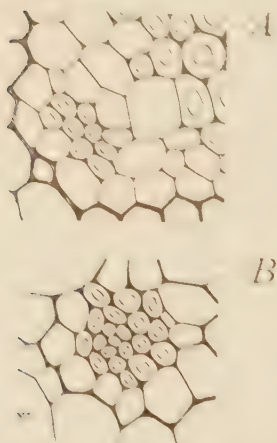


FIG. 6.—Two sections of same leaf trace: *A*, just inside endodermis of stele; *B*, 0.5 mm. outside endodermis and 1.5 mm. higher up in stem.

All of the lignified elements have spiral thickenings. In macerated preparations some of these were found to be true vessels and others tracheids. Some of these tracheids were very short, being about ten times as long as wide. No cells could be found in the leaf bundle proper or in the leaf trace that could properly be called phloem. In leaves less than one year old there was no well defined endodermis, but there was a sharp line of demarcation between the tracheids and the abutting cells. In the two-year old leaves the endodermis was well defined. In leaves older than this the thickening of the adjacent cells was extended from one to two cells farther out. The endodermis is continued in the leaf trace,

but disappears as the trace passes through the endodermis of the stele (fig. 7).

Discussion

At the present time there are two views regarding the number of categories which should be made of the parts of the plant body. The older view, and the one most generally held, is that the plant body should be divided into roots, stem, and leaves. The more recent view is that the plant consists of roots and leaves. This latter ground is taken on the interpretation of the stele as being composed of leaf traces. In other words, the stem is made up of aggregated leaf bases. Whether this interpretation is justifiable

in phyllosiphonic plants, I cannot say. The scope of this investigation does not permit of an answer, but probably those who take this view disregard the telescoping of the stem which is so common in the higher plants. From this study of *Lycopodium* as a representative of cladosiphonic plants, however, I am convinced that this interpretation for this group is not supported by the facts. In *Lycopodium* the very primitive radial stele is mapped out in

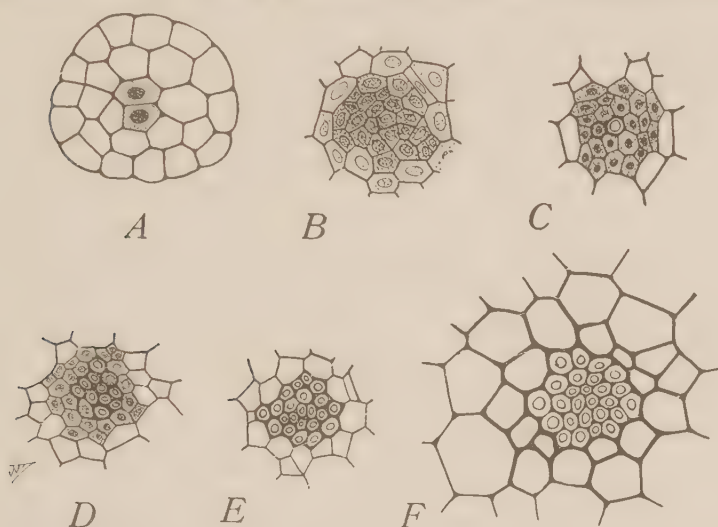


FIG. 7.—Cross-sections of leaf bundle in different stages of development: *A*, beginning of desmogen strand in primordium; *B*, desmogen strand practically completed; *C*, beginning of lignification, showing mesarch character of bundle; *D*, bundle partially lignified, showing outward progression of process; *E*, bundle completely lignified but with no endodermis; *F*, bundle from two-year old leaf with well defined endodermis.

the sporeling from the beginning, and continues to develop from an independent group of meristomatic cells so long as the plant continues to grow. This continuous stele is interrupted only by branches, and these originate by a division of the independent apical group. The vascular system of the leaves originates independently of the stele, and connects with it only by a differentiation of cortical elements. *Lycopodium*, at least, has a stem.

On the other hand, it seems that too much stress has been laid on the necessity of exactly delimiting the categories. They should

be considered as composite parts of a unified whole, rather than as separate parts making up a whole. To illustrate, the major part of the leaf trace, in its origin, belongs to the stem; but through differentiation it becomes, to all intents and purposes, an integral part of the foliar system. It may be considered as either stem or leaf, or as both stem and leaf. The same may be said for the outer layer of the cortex. By origin, it is stem; by activation, due to the formation of leaf primordia, it becomes leaf; by subsequent elongation, it again becomes a part of the stem. Where does it belong?

The direction of the differentiation in the leaf trace is a subject which deserves more attention than has been given to it. No positive statement has been found in the literature that the differentiation proceeds in either direction. Various writers speak in a vague way of the leaf trace entering the stele or passing out into the leaf; apparently the use of the terms depended upon the subject under discussion. When speaking of the stele, the leaf trace passes out; when speaking of the leaf, the trace passes into the stele. The fact is the trace passes neither in nor out. The cells composing it are laid down in place as a result of divisions in meristematic cells. The progress of the differentiation of these cells may be either in or out. In *Lycopodium* the differentiation begins in the leaf base and passes in toward the stele. What it may do in the other groups of plants is not clear from any evidence discovered in the literature on the subject.

Summary

1. The central cylinder originates independently of the leaf traces from a group of meristematic cells situated just below the apex.
2. The central stele is an exarch radial protostele consisting of alternating plates of phloem and xylem.
3. There is no sharp differentiation between the protoxylem and metaxylem, the later-forming protoxylem having the structural characters of metaxylem.
4. The differentiation of the phloem proceeds much more slowly than that of the xylem.

5. The desmogen strand of the leaf originates independently, from a group of cells in the base of the leaf primordium. Only at a later period does it join the stele by a differentiation of cortical elements.

6. The foliar bundle is mesarch, and is made up exclusively of spiral elements.

The writer wishes to express his appreciation and gratitude to Dr. W. J. G. LAND for advice and criticism, and particularly for his kindly encouragement during the progress of the investigation.

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